Title: Ecosystem scenarios shape fishermen spatial behavior. The case of the Peruvian anchovy fishery in the Northern Humboldt Current system.

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Abstract

A major goal in marine ecology is the understanding of the interactions between the dynamics of the different ecosystem components, from physics to top predators. While fishermen are among the main top predators at sea, almost none of the existing studies on ecology from physics to top predators contemplate fishermen as part of the system. The present work focuses on the coastal processes in the Northern Humboldt Current System, which encompasses both an intense climatic variability and the largest monospecific fishery of the world. From concomitant satellite, acoustic survey and Vessel Monitoring System data (~90000 fishing trips) for a ten-year period (2000-2009), we quantify the associations between the dynamics of the spatial behavior of fishermen, environmental conditions and anchovy (*Engraulis ringens*) biomass and spatial distribution. Using multivariate statistical analyses we show that environmental and anchovy conditions do significantly shape fishermen spatial behavior and present evidences that environmental fluctuations smoothed out along trophic levels. We propose a retrospective analysis of the study period in the light of the ecosystem scenarios evidenced and we finally discuss the potential use of fishermen spatial behavior as ecosystem indicator.

Highlights

Relationships between the environment, fish and fishermen were quantified in the Northern Humboldt Current System.

Ecosystem scenarios do shape fishing spatial behavior.

Environmental fluctuations are smoothed out along trophic levels

We propose ecosystem scenarios and fishermen response to each of them.

Keywords

Environmental conditions; fish distribution; coastal processes; anchoveta *Engraulis ringens;* oxygen minimum zone; vessel monitoring system; fishers.

1. Introduction

Marine ecosystems are highly structured in space (Margalef, 1979) and pelagic ecosystems, where habitats are made of constantly moving water masses, are also highly dynamic in time (Levin, 1992; Fréon and Misund, 1999). Because those natural systems tend to be out of balance (Pimm, 1991), it is fundamental to consider their spatio-temporal variability to understand the relative contributions of bottom-up and top-down controls in their functioning (Matson and

Hunter, 1992; Gripenberg and Roslin, 2007; Polishchuk *et al.*, 2013). Also, in general, since each organism tends to feed on smaller organisms, the high-frequency environmental variations tend to smooth out along trophic levels (Mann and Lazier, 2006).

Observation limitations to examine such processes have been largely overcome in the last decades thanks to new technologies and ecosystem models. There are now, in several ecosystems, spatially explicit data on abiotic factors, prey and predator distribution and abundance at high time resolution (Costa, 1993; Decker and O'Dor, 2003; Boyd *et al.*, 2004; Rutz and Hays, 2009; Bograd *et al.*, 2010). Recent works studied the linkages between environmental conditions, prey distribution and predators' behavior in time and space. The predators studied included sea mammals (Croll *et al.*, 2005; Stevick *et al.*, 2008; Cotté and Guinet, 2011; Hazen *et al.*, 2011; Santora *et al.*, 2012; Thompson *et al.*, 2012), seabirds (Embling *et al.*, 2012; Santora *et al.*, 2012; Thompson *et al.*, 2012) and fish (Thompson *et al.*, 2012; Embling *et al.*, 2013).

Those studies identified critical processes and key areas that can be directly useful in conservation, marine spatial planning, or in the management of human activities in marine ecosystems. Nevertheless, while fishing represents world catches of ~89.8 million of tonnes per year (between 2006 and 2011; FAO, 2012) and competes directly with natural predators, none of those studies on spatial ecology from physics to top predators contemplated fishermen as part of the system. Admittedly, fishermen are peculiar top predators because they rely on technology and are driven by a distinct currency than that of natural predators. Nonetheless, in pelagic ecosystems water masses and fish schools are constantly moving (Swartzman *et al.*, 2008; Peraltilla and Bertrand, 2014). Thus, fishermen do face the same uncertainty on prey localization as natural predators do and their spatial behavior reflects their need for solving the same challenge. In that sense, it has been shown that fishermen in the Peruvian anchovy fishery deploy similar spatial foraging strategies to those of other animal predators (Bertrand *et al.*, 2007).

The Northern Humboldt Current System (NHCS) off Peru provides a great opportunity for studying the association between the dynamics of ecosystem components in a bottom-up-controlled exploited ecosystem (Ayón *et al.*, 2008; Bertrand *et al.*, 2008a). The NHCS is characterized by an intense variability from secular to intra-seasonal timescales. Variations of the Eastern Pacific intertropical convergence zone or the Pacific decadal oscillation can impact the NHCS at inter-decadal and secular scales (Chavez *et al.*, 2003; Gutierrez *et al.*, 2009; Salvatecci *et al.*, 2012). At inter-annual scales, El Niño Southern Oscillation – characterized by relatively warm/cold El Niño / La Niña events – has a strong effect on the eastern south Pacific region (Colas *et al.*, 2008; Takahashi *et al.*, 2011; Dewitte *et al.*, 2012; among others). At seasonal and intra-seasonal scales, the NHCS is mostly modulated by wave dynamics of equatorial origin and local wind forcing (Penven *et al.*, 2005; Echevin *et al.*, 2011, 2014; Dewitte *et al.*, 2012; Chaigneau *et*

al., 2013; Pietri *et al*., 2014). The resulting environmental scenarios directly determine the extent of the tridimensional anchovy habitat (Bertrand *et al*., 2004a, 2011), which in turn conditions fish availability for the main predators in this system, the fishermen (Bertrand *et al*., 2008a). Besides, the NHCS produces more fish per unit area than any other region in the world oceans and sustains the world's largest monospecific fishery (Peruvian anchovy or anchoveta, *Engraulis ringens*). To cope with the intense climatic variability, the management of the anchovy fishery is adaptive, i.e. catch limits are re-assessed every ~6 months and opening and closure periods decided on the basis of daily monitoring of the ecosystem, the fish population and the fishery (Chavez *et al*., 2008). The Peruvian Marine Research Institute (IMARPE) is in charge of this intense monitoring. It comprises satellite information on environmental conditions (e.g. sea surface temperature, chlorophyll-a and sea level anomaly, among others) at daily and weekly resolutions. Fish population distribution and biomass are monitored through scientific acoustic surveys (two to three times a year). The fishing activity is supervised through landing statistics, Vessel Monitoring System (VMS) and on-board observers reports (Bertrand *et al*., 2008b; Joo *et al*., 2011). The amount of available data makes the NHCS a highly appealing ecosystem for an integrated approach on ecosystem dynamics. In this highly-variable and data-rich ecosystem, Bertrand *et al*. (2008a) analyzed how large-scale oceanic forcing, via Kelvin waves, affected the coastal ecosystem (from oceanography to fishermen). They pioneered the incorporation of fishermen as a top predator for studying ecological dynamics and proposed contrasting scenarios of coastal oceanography, anchovy distribution and fishing activity, during the passage of coastally trapped upwelling and downwelling Kelvin waves.

The present work focuses more closely on the coastal processes in the NHCS, and on the spatial response of fishermen to varying environmental and anchovy conditions. In particular, we explore and quantify the associations between the dynamics of three ecosystem compartments: environmental conditions (Environment), anchovy biomass and distribution (Anchovy) and fishermen spatial behavior (Fishermen), for a ten-year period (2000-2009). Data on Environment and Anchovy were obtained from acoustic surveys performed by IMARPE and satellite observations. Data on Fishermen were based on VMS data (~90000 fishing trips from 2000 to 2009), processed with a state-space model so that the nature of the behavior in which fishermen are engaged is known at each position (Joo *et al*., 2013). The existent evidence of bottom-up forcing in the NHCS (Ayón *et al*., 2008; Bertrand *et al*., 2008a) indicates that strong Environment-Anchovy and Anchovy-Fishermen associations should be expected. Since Fishermen have shown similar spatial foraging strategies to those of other predators (Bertrand *et al*., 2007), we hypothesize that – as for other predators – their spatial behavior responds to prey and environmental conditions. Then, significant Environment-Fishermen associations are expected, though not as strong as for Anchovy and Fishermen (direct prey-predator relationship). The studied decade does not encompass strong ENSO (El Niño Southern Oscillation) events. Season is thus

expected to be the main scale of variability for environmental conditions. We tested for differences between two seasonal modes, summer and spring/winter, within each ecological compartment and analyzed trends separately for each seasonal mode. We eventually propose ecosystem scenarios based on the linkages evidenced between the three compartments and discuss the potential use of fishermen spatial behavior as ecosystem indicator.

2. **Materials and Methods**

We focused on several time-periods from 2000 to 2009 such that concomitant data on the environment, fisheries acoustic and VMS were available. In total, 16 time-periods were available, 6 in austral summer and 10 in austral winter/spring (Table 1). Since only one value per time-period was obtained for each Anchovy descriptor, one representative value per time-period was computed for each Environment and Fishermen descriptor. This measure allowed for multivariate analyses involving the three compartments.

2.1. Environmental data

For each time-period, we produced a description of the environment as detailed in Table 2. We used sea surface temperature (SST) from the AVHRR sensor of NOAA satellites from 2000 to 2009. The chlorophyll-a (CHL) satellite data from 2000 to 2007 were obtained from the SeaWiFS sensor and from 2008 to 2009 from the MODIS sensor. In order to correct the MODIS CHL data from significant departures from the better calibrated SeaWIFS sensor, the seasonal and spatial differences were previously computed during the common period between both sensors (2003-2007) and then applied to the 2008-2009 MODIS data. All satellite data, initially at a spatial resolution of 4 km and a weekly time resolution, were averaged the entire time period and the whole study area (from 3°S to 16°S and from the shore up to the 2500 m isobath) to obtain one representative value per time-period (Table 1).

To account for the vertical distribution of the oxygen minimum zone (OMZ), a critical parameter of the NHCS (Bertrand *et al*., 2011), we computed the depth of the oxycline (OXY), i.e. the depth at which the dissolved oxygen equals 2 mL L^{-1}. All measurements were made from Niskin bottles and CTD data sampled during IMARPE scientific surveys. For each time-period, the mean oxycline depth was computed as a weighted average of monthly values, taking into account the number of observations per month. Those observations correspond to a latitudinal range between 7°S and 16°S. A sharp change in oxygen concentration and oxygen minimum zone intensity occurs at ca. 7ºS (Fuenzalida *et al*., 2009; Bertrand *et al*., 2010). North of 7ºS the intensity of the OMZ is highly variable and depends on the dynamics of Tropical/Equatorial water masses.

The range 7ºS - 16ºS provides a more robust proxy of oxygen condition where most of the anchovy is distributed (i.e. not in Tropical/Equatorial water masses).

2.2. Anchovy data

Since 1983, IMARPE has been conducting on average two acoustic surveys per year to monitor fish population distribution and biomass. These surveys consist of parallel cross-shore transects of ~100 nm long, with a ~15 nm inter-transect spacing. Simrad (kongsberg Maritime AS, Norway) scientific echosounders working at several frequencies are used to estimate biomasses (see Gutiérrez *et al*., 2007; Castillo *et al*., 2009; Simmonds *et al*., 2009). An extensive midwater-trawl sampling completes the acoustic surveys for species identification. The nautical-area-backscattering coefficient (NASC, in m^2 mn^{-2}), an index of fish biomass (Simmonds and MacLennan, 2005), is recorded at each georeferenced elementary distance sampling unit (EDSU) of 1 nm. From each acoustic survey, we extracted five descriptors of the spatial distribution of anchovy (Table 2): (i) the mean anchovy NASC, used as an index of fish biomass (s_A); (ii) an index of local biomass (s_A+), i.e. the mean anchovy NASC for the set of ESDUs with non-zero fish biomass; (iii) an index of spatial occupation (ISO), i.e. the percentage of ESDU with anchovy; and (iv) the center of gravity and the inertia of the distance to the coast of anchovy NASC (DC and I, respectively).

2.3. Fishermen spatial behavior

The pelagic fishery in the NHCS is mono-specific, since anchovy represents 95% of the total catches (Fréon *et al*., 2008). The anchovy fishing trips, which exclusively aim at fishing anchovy, constitute the world's largest mono-specific fishery (average annual catch of 6.8 millions of tonnes between 2000 and 2011; FAO, 2013). The fishing activity in the NHCS is monitored by IMARPE through landing statistics, VMS and on-board observers' data. Since 2000, VMS records precise geographical positions once an hour for the entire industrial fleet. Only fishing trips from the industrial fleet along the north-center (3ºS-16ºS) Peruvian coast were considered for the analysis (the southern region was excluded because of its lesser contribution to the catches and a different management policy). We report in Table 1 the number of fishing trips documented for each time-period.

Pre-processing of VMS data was performed as described in Bertrand *et al*. (2005, 2007) and Joo *et al*. (2011). We identified positions at sea or at port based on their distance to the nearest port and their speed. We considered each series of consecutive positions at sea as a trip. To select fishing trips only, we excluded trips with a minimum speed greater than 3 knots (indicating the impossibility of fishing activity). To exclude the few trips targeting other pelagic species (e.g.

jack mackerel), trips from vessels with fishing authorization for multiple species and lasting more than 5 days were not considered (anchovy fishing trips typically last ~24 hours).

Eventually, for each fishing trip, the following global indicators were computed: the duration (Dur), the total distance traveled (Dist) and the maximum distance from the coast (Max.DC). Additionally, we used two metrics, k and sigma, that characterize the geometry of the fishermen movements (Bertrand *et al.*, in review). They are derived from the fit of a Generalized Pareto random walk model to the move-length distribution displayed by fishing trip trajectories. This random walk model involves two parameters of interest: a shape parameter k which characterizes the movement diffusion (finite and light tails with normal diffusion patterns for k<0, and k between 0 and 0.5, respectively, and heavy tails with super diffusion patterns for k>0.5), and a scale parameter sigma (where sigma>0) which relates to the average length of the moves used to search for fish. Super diffusion is characterized by the mixing of rare, long and relatively straight movements with movement bouts composed of short moves and high turning rates (Dubkov *et al.*, 2008). Metrics k and sigma were computed for each vessel from the fishing trips performed within each time-period.

Another source of information regarding fishing activities comes from the program of on-board observers 'Bitácoras de Pesca' deployed by IMARPE. For ~1% of the fishing trips, on-board observers record the location and time of three main activities occurring during the trips: fishing, searching and cruising. In order to infer the activities for the remaining 99% of the fishing trips, a supervised hidden semi-Markov model was trained and validated using the on-board observer dataset (Joo *et al.*, 2013). This model reached a mean accuracy of 80% in the determination of the correct activities from the VMS data. From the reconstructed sequence of fishing activities, we computed four additional features: the proportion of time spent searching (Searching), fishing (Fishing) and cruising (Cruising), and the time spent from the beginning of the trip until the first fishing set (Bef.Fishing).

For the multivariate analyses, we computed a median per time-period over all fishing vessels for each descriptor.

2.4. Statistical analyses

A synoptic sketch of the statistical analyses between the ecosystem compartments is reported in Figure 1. After pre-processing the data, univariate statistics were computed for each variable to test for differences between seasonal modes and characterize overall tendencies and potentially remarkable time-periods. The Wilcoxon rank sum test (Wilcoxon, 1945) was performed

for testing for mean differences between summer and winter/spring periods. This test is one of the best non-parametric alternatives to the t-test when its assumptions are not met (at least 95% of statistical power compared to the t-test when assumptions are met; Siegel, 1956). Trends were computed using least trimmed squares robust regression (Rousseeuw, 1984). It is based on the subset of h observations (out of n) whose least squares fit possesses the smallest sum of squared residuals. The parameter h is computed as n/2 + (p+1)/2 (Rouseeuw, 1984), where p is the number of explanatory variables (equal to 1 in our case).

For multivariate analyses, all variables were standardized (Z-scores). Since we first aimed at characterizing each compartment and then associations between them, we first carried out a Principal Component Analysis (PCA; Pearson, 1901; Husson *et al*., 2010) for each compartment at the scale of the time-periods. These PCAs identify the main modes of variability. For quantifying the linear association between the first principal component of Environment, Anchovy and Fishermen, we computed Kendall's Tau rank correlation coefficients (Kendall, 1938; Siegel, 1956) between each pair of first components. Kendall's Tau was preferred as correlation coefficient since it allows computing asymptotically distribution-free confidence intervals (Hollander and Wolfe, 1999).

In addition to Kendall's tau, the overall association between each pair of compartments (Environment and Anchovy, Anchovy and Fishermen, and Environment and Fishermen) was analyzed through RV coefficients (Escoufier, 1973). The RV coefficient is a multivariate generalization of the squared Pearson correlation coefficient. RV values range between 0 and 1, where 0 means no association and 1 means perfect association. Confidence intervals were computed using a bootstrap procedure (Claude, 2008) at a 90% confidence level. The significance of the RV coefficient was estimated by means of a permutation test (Heo and Gabriel, 1998).

We also performed a multiple coinertia analysis (Chessel and Hanafi, 1996) between the three PCAs. This is a multivariate method for coupling k tables (k>2) sharing the same rows (individuals or variables). The tables must be previously analyzed by separate inertia analyses (for instance, PCAs). With the multiple coinertia analysis, we aim at resorting a synoptic understanding of the three compartments by: (i) calculating a synthetic table representing the common structure of the PCAs, and (ii) projecting individuals (i.e. time-periods) and variables from the three ecosystem compartments in a common space. Tables are weighted equally for the multiple coinertia analysis. Finally, we performed a hierarchical clustering on the scores of the time-periods in the synthetic table with a view to discriminating groups of time-periods.

Statistical analyses were performed with R software (R Core Team, 2013). Robustbase package (Rousseeuw *et al*., 2012) was used for least trimmed regression, FactoMineR package

(Husson *et al.*, 2013) was used for PCA and ade4 (Dray *et al.*, 2007) for multiple coinertia analyses, and the stats package (R Core Team, 2013) for the hierarchical clustering analysis.

3. Results

3.1. Univariate analyses

Series of environmental conditions are shown in Figure 2a-c. SST and CHL values were greater in summer than in winter/spring periods ($p<0.001$ for both variables) and exhibited increasing trends ($p<0.01$ for both variables) on winter/spring periods. The differences in SST and CHL between seasons were larger at the first half of the series than at the second half. For OXY no significant differences between seasons were observed and no trend was observed either. Still, the October - December 2003 time-period (denoted 2003/10-12 hereafter) was characterized by a remarkably deep oxycline.

Fish distribution also varied in time (Fig. 2d-h). The s_A+ and s_A indexes differed significantly among seasonal modes ($p<0.01$) and an increasing trend ($p<0.01$) was observed for s_A+ in winter/spring periods. Two periods presenting the greatest s_A (and s_A+) values lied out of the general trend: 2008/02-04 and 2002/02-03. The former period, 2008/02-04, along with 2003/10-12, were also characterized by the lowest ISO. Finally, 2000/06-07, 2000/10-11 and 2001/10-11 had the greatest DC and I features.

Since hundreds of fishing trips were comprised in each time-period (Table 1), we analyzed the temporal evolution of both the median values and the distribution of each Fishermen variable. In order to facilitate visualization, the values associated with the greatest occurrences are shown in Figure 3. The complete range of values is available in Figure A.1 in Appendix A.

Only Cruising showed significant differences between seasonal modes ($p<0.01$). Therefore, for Fishermen variables robust trends were computed for the whole series without discriminating between seasonal modes. Negative trends were observed for Dur, Dist, Bef.Fishing, Cruising and sigma ($p<0.0001$). By contrast, Searching, Fishing and k reported increasing trends ($p<0.0001$). 2001/10-11, 2003/10-12 and to a lesser extent 2002/10-11 presented the greatest values for Dur, Dist, Max.DC, Bef.Fishing and Cruising, and 2001/10-11 and 2003/10-12 presented the greatest variability for Dur, Dist, Max.DC, Bef.Fishing (cf. distributions in Fig. 3a,b,c,d). Conversely, in 2002/02-03, Dist, Max.DC, Bef.Fishing and Cruising were low and Fishing was high.

3.2 Multivariate Analyses

Significant correlations between variables and principal components are shown in Table 3. We also present the scores of each time-period for the first principal components (Fig. 4).

3.2.1. Environmental conditions

In the Environment PCA, the first principal component, which accounted for 75% of the variance, was positively correlated with CHL and SST, and negatively with OXY (Table 3 and Fig. A.2 in Appendix A). These relations mainly refer to the seasonal cycles. During summer, waters are warmer (greater SST values), and due to a reduced cloud cover, more light penetrates into the water column, what positively impacts the productivity at sea (higher CHL; Echevin *et al.*, 2008). The thermocline and oxycline are also shallower during summer (lower OXY; Gutiérrez *et al.*, 2011). The opposite phenomenon occurs during winter. The reported scores reflected the seasonality: all summer periods had greater scores than winter and spring periods (Fig. 4; $p<0.001$ for differences in scores between seasonal modes). Nonetheless, the intensity of the seasonality (difference summer – winter/spring) was reduced during the second half of the series. This was accounted for by fitting a linear regression to the scores and computing the sums of squared residuals for the first and second half of the series. Large differences were found (10.9 vs. 1.2, for first and second half, respectively; Table B). The second principal component represented 21% of the variance and was significantly correlated with OXY (Table 3). This component did not reflect a significant seasonality. Although the temporal variability of the oxycline depth is partly related to the seasonal cycle, specific large scale forcing events such as downwelling Kelvin waves can deepen the oxycline (Gutiérrez *et al.*, 2008). Within the studied period, 2003/10-12 and 2007/02-04 had the lowest scores (deepest oxycline depth) for this component (Fig. 4).

3.2.2. Anchovy distribution

The first principal component, accounting for 60% of the variance, was positively correlated with s_A and s_A+, and negatively correlated with DC and I (Table 3 and Figure A.3 in Appendix A). This axis can be interpreted as an index of fish biomass and proximity to the coast. Scores reflected, although with less intensity, the seasonality observed in the first axis of the Environment PCA (Fig. 4; $p<0.01$). A significant increasing trend over time was observed for this first component ($p<0.01$) through a linear regression. The second component, explaining 23% of the variance, was significantly correlated to ISO (Table 3). It can be seen as fish evenness, and it should be interpreted considering the scenarios in terms of s_A, s_A+ and DC: high evenness is favorable to fishermen activity if the global biomass is high, since there is lot of anchovy everywhere. On the opposite, if the biomass is low, a high evenness means highly dispersed anchovy (low s_A+), which are difficult to catch (Bertrand *et al.*, 2004b). The latter scenario corresponds to 2003/10-12, which had by far the lowest score (Fig. 4).

3.2.3. Fishermen spatial behavior

Due to the relatively large number of variables for a small number of individuals, we discarded from the multivariate analyses the variables presenting very strong correlations (r>0.9; i.e. Dist., Bef.Fishing and Dur, all of them strongly correlated with Cruising). We also discarded Searching since the proportions of the time spent Cruising, Fishing and Searching sum to one (no variable should be expressed as a linear combination of others). Overall, we used Max.DC, Fishing, Cruising, k and sigma. The other variables were still used as supplementary variables and projected in the PCA space (Fig. A.4 in Appendix A). The first principal component, explaining 71% of the variance (Table 3), refers to fishermen activity budget, which indicates the investment in energy and time necessary for their activities (Altmann, 1974; Defler, 1995). High values on this activity budget axis correspond to ‘cheap foraging’ (more time is allocated to searching and fishing than to cruising), while low values indicate ‘expensive foraging’ (more time is dedicated to cruising, longer distances are traveled, more time is spent before the first fishing set, farther distances from the coast are traveled). Scores showed an increasing linear trend (towards ‘cheap foraging’) with time ($p<0.0001$; Fig. 4). Those scores are coherent with the overall increasing 'efficiency' shown by the fishermen through the years (i.e., increasing trend in daily catches and decreasing trend in the number of fishing days until the quota was filled, until the individual vessel quota system was established; IMARPE, 2013). The second principal component (not shown) accounted for 23% of the variance (Table 3). It had significant correlations with only two variables (k and Max.DC) and could not be properly interpreted.

3.2.4. Environment vs. Anchovy vs. Fishermen

Regarding the association between the first principal components only, the activity budget component of Fishermen PCA was strongly correlated with the fish biomass and proximity component of Anchovy PCA (0.65 ± 0.20; $p<0.001$). The latter was also correlated with the seasonal cycle component of Environment PCA (0.68 ± 0.18; $p<0.0001$). Likewise, the seasonal cycle was positively correlated with activity budget (0.60 ± 0.25; $p<0.001$). However, none of these correlations is statistically greater than the others, since their confidence intervals overlap. The three RV coefficients were also strong, i.e. Environment and Anchovy (0.61; $p<0.001$), Anchovy and Fishermen (0.63; $p<0.001$) and Environment and Fishermen (0.56; $p<0.01$). Their 90% confidence intervals overlapped: <0.28,0.65>, <0.37,0.63> and <0.29,0.59>, for Environment and Anchovy, Anchovy and Fishermen, and Environment and Fishermen, respectively. Nevertheless, those significant associations provide a powerful way to quantify the strength of the relationships between the ecosystem compartments.

A multiple coinertia analysis was applied to Environment, Anchovy and Fishermen PCAs (Fig. 5; Table 4). The multiple coinertia space was composed of two axes, accounting for 73% and 17% of the variance each. The interpretation of the graphical projection of the variables on the coinertia space (Fig. 5; left panel) is analogous to that on a PCA space (see Fig. A.2, A.3, A.4 in Appendix A). High SST and CHL values were strongly related to high s_A+ (local biomass), high Fishing, low Cruising, low DC and I (distance from the coast of anchovy and its inertia). To a lesser extent, high SST and CHL were also related to high s_A and low Max.DC (distance to the coast of fishermen). Deep oxycline (OXY) was partly associated with low s_A and ISO (anchovy spatial occupation), and high Max.DC. Low ISO was also associated with high k (diffusivity of fishermen movements).

Regarding the time-periods, a hierarchical clustering analysis was performed. Based on the computed dendrogram (Fig. A.5 in Appendix A) and the explained variance (i.e. the percentage of total variance represented by the between-cluster variance; Husson *et al*. 2010; Table A.2 in Appendix A), the 4-cluster structure, which accounted for 80% of the explained variance, was retained. The time-periods that correspond to each cluster are represented by distinct colors in Figure 5 (right panel). Because of the great variability within each cluster, we characterized only one time-period per cluster. We chose the ones that stood out in the preceding analyses: 2008/02-04, 2002/02-03, 2003/10-12 (the only period in its cluster) and 2001/10-11. 2002/02-03 was characterized by a superficial OXY, very large ISO and s_A values, and to a lesser extent, high SST, CHL, s_A+ and Fishing values. 2008/02-04 was characterized by the greatest SST, CHL, s_A+ and Fishing, and low DC, I, Cruising and Max.DC values. 2003/10-12, on the contrary, corresponded to the deepest OXY, the lowest ISO, low s_A, the highest Cruising, high Max.DC and k. 2001/10-11 corresponded to the lowest SST, the highest I, a very high ISO, the highest Max.DC and low Fishing.

4. **Discussion**

4.1 *Environment, Anchovy, Fishermen and the bottom-up transfer*

In this study, we explored and quantified the associations between the dynamics of three ecosystem compartments (Environment, Anchovy and Fishermen) and showed that ecosystem scenarios – abiotic and biotic conditions – do shape fishing spatial behavior. Most of the existent literature in fisheries deduces fish abundance and distribution from catchability indicators, making the implicit assumption that fishing effort reflects fish conditions. Only a few works have studied the actual relationships between the patterns of fisheries and their target species (e.g., Hancock *et al*., 1995; Bertrand *et al*., 2004b, 2005, 2008b). Here, we used a richer dataset in terms of the amounts

of data - 16 concomitant fishing seasons and scientific acoustic surveys – and in the nature of the variables used. To cope with the uncertainties and complexities related to data from different sources, sampling methods and scales, the analyses were kept as simple as possible: the scale of analysis was constrained by the lowest resolution of the available data and exploratory methods were used.

A major drawback related to our dataset – as mentioned above – is that we did not have both summer and winter/spring periods for all years. Moreover, winter/spring periods did not always comprise the same months (e.g., 06-07 and 10-11). Therefore, the trends fitted should only be used for interpreting the variations experienced during the studied time-periods; not as increasing SST and CHL trends for the whole 2000-2009 decade. When compared with complete monthly 2000-2009 series, no linear trend in winter was found for SST nor CHL. However, we did find a reduction in the intensity of the seasonality in the second half of the decade, observed in Fig. 2a-b and Fig. 4.

Regarding the associations between ecosystem compartments, the three pairwise associations were statistically significant. Concerning point estimates, Environment-Anchovy and Anchovy-Fishermen links were the strongest compared with the least direct one (Environment-Fishermen) whatever the metric considered (RV and Kendall's tau). We cannot conclude on the superiority of the direct links since the confidence intervals overlapped. The computation of confidence intervals was strongly penalized by the low number of observations (Hollander and Wolfer, 1999). Gathering data from more time-periods could contribute to reduce confidence intervals and improve correlation estimates.

Nevertheless, our findings are consistent with a bottom-up transfer that was already evidenced by Bertrand *et al*. (2008a) when analyzing the effect of upwelling and downwelling Kelvin waves on several descriptors of the Peruvian coastal oceanography, anchovy distribution and fishing fleet behavior. They characterized contrasting ecological scenarios that corresponded to strong El Niño events (warm scenarios) and to average upwelling periods (cold scenarios).

Unlike Bertrand *et al*. (2008a), we focus on the coastal processes of the NHCS, and our studied period, 2000-2009, does not encompass strong El Niño events, but only 'weak' events (2002-03, 2004-05 and 2009-10). These events correspond to 'El Niño Modoki' or 'Central Pacific El Niño' that are distinct from the extraordinary warm events such as the ones from 1982-83 and 1997-98 (Takahashi *et al*., 2011). When Central Pacific El Niño occurs, the conditions off Peru can even be slightly cooler than average (Dewitte *et al*., 2012), far from the archetypal El Niño effects on the Peruvian ecosystem (Barber and Chavez, 1983; Alheit and Ñiquen, 2004; Bertrand *et al*., 2004a, Ñiquen and Bouchon, 2004). The studied period therefore lies within the dominant

ecosystem state corresponding to an average 'upwelling dominant scenario' without extreme El Niño events (Bertrand *et al.*, 2008a). Indeed, 'El Niño Modoki' did not show to impact on fishermen behavior. In this context, the seasonal scale becomes the scale of greatest environmental variability.

An important contribution of our work concerns the Fishermen compartment. Based on statistics computed from an unprecedented rich dataset (spatially-explicit data from ~90000 fishing trips), we showed that Fishermen spatial behavior could be seen as a function of anchovy biomass and distribution, and environmental conditions. Fishermen-Anchovy association (RV=0.63) suggested that, despite the available technology and all the economic drivers involved in fishermen behavior, uncertainty on prey location is a major driver of their spatial behavior. This finding supports the evidence that fishermen deploy spatial foraging strategies comparable to that of other animal predators (Bertrand *et al.*, 2007). Fishermen-Environment association was not at all despicable (RV=0.56), showing that fishermen behavior is sensitive to changes in environmental conditions, most likely through transfer via Anchovy (RV=0.61 for Environment-Anchovy). The association between Environment and Fishermen is regarded as an indirect link, since Fishermen are not directly shaped by the Environment: SST, CHL and OXY only affect Fishermen through their effects on anchovy biomass and distribution. Moreover, in the NHCS off Peru, there are no extreme weather conditions that could affect fishermen tactics and strategies directly.

Looking closely at the trends of the first principal components (Fig. 4), the strong seasonality observed for Environment (seasonal cycle component) is less pronounced for Anchovy (fish biomass and proximity) and almost unnoticeable for Fishermen (activity budget). Conversely, the marked increasing trend observed for Fishermen, seemed to be occluded for Anchovy and then for Environment by the seasonal variability. These results are regarded as empirical evidence of high-frequency environmental variations being smoothed out through trophic levels (Mann and Lazier, 2006; Di Lorenzo and Ohman, 2013). Future studies based on the analysis of longer time series, with more regularly-sampled time-periods (with at least one winter and one spring/summer period per year), could provide a definitive statistical demonstration of this result.

How environmental fluctuations influence population dynamics and animal behavior are questions that have been examined in several studies. McManus and Woodson (2012) showed that the more organism size and motility increase, the weaker are the relations between organism behavior and physical processes. Other studies (e.g. Miramontes and Rohani, 1998; Petchey, 2000; Greenman and Benton, 2003) showed transfer of environmental variability in *ex situ* and theoretical populations. Rouyer *et al.* (2012) showed, using empirical data, that mortality of larger fish lead to more prevalent short-term fluctuations in fish populations. However, to our knowledge, no work had shown empirical evidences of smoothed out transfer through several ecosystem

compartments, from the environment to top predators. Here we provide – for the first time – empirical evidence of (1) bottom-up and smoothed out transfer of the high-frequency environmental fluctuations through the main compartments of an ecosystem (i.e. seasonal effect through Environment-Anchovy-Fishermen); and (2) magnification of low-frequency fluctuations by trophic transfer (i.e. magnified temporal trends through Fishermen-Anchovy-Environment). Furthermore, after the first half of the time-series, the scores of the first component of Environment and, to a lesser extent, Anchovy and then Fishermen, showed a weaker variability though continued showing a positive trend (Fig. 4). For each compartment, the variability – computed as the sum of squared residuals from a fitted linear regression – was greater during the first half of the studied series than after (Table A.3 in Appendix A). Moreover, variability values decreased when rising into the ecological levels.

4.2 Fishermen response to ecosystem scenarios

Based on the statistical analyses, we identified four ecosystem scenarios (Fig. 6). Each scenario involved a distinct cluster in the coinertia space (Fig. 5, right panel). The first two scenarios corresponded to favorable ecosystem conditions and are associated with the time-periods 2002/02-03 and 2008/02-04 while the third and fourth are less favorable and can be illustrated by the time-periods 2003/10-12 and 2001/10-11. Here, we analyze and discuss those scenarios taking into account that changes in biomass of organisms and in environmental conditions are not always simultaneous. Whereas unfavorable environmental conditions can trigger mortality and translate into low biomass almost instantaneously, favorable environmental conditions will affect recruitment, producing increased population biomass with delay. By contrast, patterns of geographic distribution or organism movements may adjust rapidly to physical forcing (Bertrand *et al.*, 2008a).

4.2.1 The favorable scenarios

Scenarios I and II (Fig. 6, upper panels), illustrated by the time-periods 2002/02-03 and 2008/02-04, were characterized by relatively high SST (relatively to the range of temperatures encompassed in our dataset), high primary production and a shallow oxycline. Under both scenarios, anchovy was abundant and close to the coast. High SST and CHL values characterized productive summertime conditions (Echevin *et al.*, 2008; Gutiérrez *et al.*, 2011) with cold coastal waters close to the coast that favored locally-concentrated anchovy biomass (Gutiérrez *et al.*, 2007; Swartzman *et al.*, 2008). Evidence of negative relation between anchovy acoustic biomass and oxycline depth was also shown by Bertrand *et al.* (2011). They suggested that anchovy is capable of surviving in areas where the oxygen minimum zone is very shallow, where they escape from predation by larger fish that need more oxygen, and forage on prey concentrated over a thin

surface layer. The two scenarios described above represent favorable conditions for fishermen because fish is easily catchable. Overall, fishermen had an efficient activity budget: more time was spent fishing rather than cruising and vessels did not need to go far from the coast. Nevertheless, in 2008/02-04 (Fig. 6, right-upper panel), local biomass was higher, and highly concentrated near the coast. Compared to 2002/02-03, this scenario was even more favorable for fishermen not only in terms of activity budget but also in terms of movement geometry. Strong patchiness of anchovy led to more diffusive spatial behavior of fishermen (Bertrand *et al*., 2005, 2007). Since anchovy patches were very close to the coast, fishermen did not need to go far to fish, so the average length of the moves was very small. Because fish was very close and highly patchy, only a small proportion of time was spent cruising; most of the time they were searching and fishing (Fig. 3). That translated into movements composed of a large proportion of small moves (searching behavior within fish aggregation) and a small proportion of large moves (straight transit between port and anchovy aggregation), creating a super diffusive, Lévy-like movement (Codling *et al*., 2008).

Conversely, in 2002/02-03 (Fig. 6, left-upper panel) anchovy was spread over more space and exhibited a lower local biomass than in 2008/02-04. That meant that, in spite of the overall availability of anchovy, it was not very patchy so it pushed fishermen to visit more patches to fill the vessel hold. Thus, the relationship rare-large-moves vs. numerous-small-moves was not observed; instead moves were about the same length, producing a normally diffusive movement. Nonetheless, fish was close to the coast, so the average length of the moves was small.

4.2.2 The unfavorable scenarios

Scenarios III and IV (Fig. 6, lower panels), illustrated by the time-periods 2003/10-12 and 2001/10-11, were characterized by relatively low SST (relatively to the range of temperatures encompassed by our dataset), low primary production and deep oxycline. In both scenarios, anchovy was scarce. Low SST and CHL characterized winter conditions (Echevin *et al*., 2008; Gutiérrez *et al*., 2011), associated to low local biomass (Gutiérrez *et al*., 2007).

2003/10-12 was the only member of its cluster, indicating it was an extreme scenario among the ones analyzed in this work. In 2003/10-12, the extent of cold coastal upwelling waters was very limited, and so was anchovy habitat (Bertrand *et al*., 2004a; Swartzman *et al*., 2008), explaining the lowest ISO of the series. Although anchovy was not too far from the coast, it was very scarce (the lowest s_A value of the series), concentrated in very few spots and most likely deep (since oxycline was remarkably deep). This corresponded to an adverse scenario for fishermen. For starters, fishermen went far from the coast and made fishing trips that lasted longer (Fig. 3) due to the scarceness of anchovy and the difficulty to find them. They spent most of the time

cruising, and low time searching and fishing. Since the scarce anchovy was concentrated (low ISO), this led to super diffusive movements (less diffusive than in Scenario II). Fishermen made few large moves – 'large' compared to the 'small' ones – looking for a zone they presumed to be of high prey density, and many small moves within these zones trying to find attractive densities of prey to fish. Since fishermen went far from the coast looking for fish, the average length of moves (large and small altogether) was higher than in Scenario II.

In 2001/10-11, the extent of cold coastal upwelling waters was high, and so was the area occupied by anchovy (Bertrand *et al.*, 2004a; Swartzman *et al.*, 2008). Anchovy distribution was even but extended very far from the coast in the form of spare aggregations. This was a difficult scenario for fishermen too, mostly expressed through the high variability in their behavior (the highest variability in most Fishermen variables; Fig. 3 and Fig. A.1 in Appendix A). In general, fishermen went farther from the coast looking for prey. Because scarce anchovy was distributed in many ESDUs, close and far from the coast, fishermen seemed to use normally diffusive movements, moving constantly between aggregations of dispersed anchovy. That spatial behavior produces inefficient activity budgets, since most of the time at sea was spent cruising between aggregations and going far from the coast, rather than fishing/searching. Moreover and as a consequence, the average length of the moves was larger.

It should be stressed that both unfavorable scenarios presented the greatest variability in fishermen spatial behavior among all the studied periods (greater in 2001/10-11 than in 2003/10-12; Fig. 3 and Fig. A.6 in Appendix A). It may evidence that in scenarios of high accessibility to prey, fishermen act more homogeneously, as it is easy for everyone to find fish and to catch it. But when conditions are difficult, each fisherman manages risks differently, and personal strategies count more. This type of behavior is likely to be enhanced in El Niño/La Niña conditions, for which a similar scenario-based analysis would be appealing.

4.3 Fishermen behavior and ecosystem approach to fisheries

This work provides a better understanding of how changes in environment and prey conditions shape fishermen behavior. We call it spatio-temporal or spatial behavior because it is characterized by spatial and temporal descriptors of fishing trips (e.g. distance traveled, maximum distance to the coast, duration of the fishing trip, time spent cruising, fishing, etc.).

As stated by Boyd *et al.* (2004), we intuitively think in terms of space and time dimensions partly because these are the easiest to measure but there are many other dimensions that characterize an animal's – or in this case human's – state. Some other variables may explain an

important part of the behavioral variability, such as the vessel holding capacity, the personality of the captain, oil and fish meal prices, technology improvements, government management measures for specific seasons, company strategies and tactics (i.e. how many vessels to deploy each day and in which zones, at which factories to land the fish), the degree of competition or cooperation between fishing vessels. Taking into account these other variables would improve our understanding of fishermen behavior, which is under the joint influence of economics, politics, oceanographic and biological conditions (Wilen, 2004). A remaining challenge is the characterization of the collective behavior, since we always consider all fishing trips as independent from the others (the same approach is usually taken in animal behavior; Boyd *et al.*, 2004). Despite we did not consider all these potential factors, we have shown that prey availability and environmental conditions already play a great and significant role in shaping fishermen behavior, at least at the scale of average characteristics of fishing trips during two or three months periods.

In synthesis, this study showed how ecosystem scenarios shape fishermen spatial behavior. We also provided empirical evidences of bottom-up and smoothed out transfer of the high-frequency environmental fluctuations and magnification of low-frequency fluctuations along the ecosystem compartments. Top predators are increasingly seen as integrators of the state of the ecosystem they inhabit (Boyd *et al.*, 2006). In the need for information to support the ecosystem approach to fisheries (EAF; Browman and Stergiou, 2004; Garcia and Cochrane, 2005; Jennings, 2005), top predators could be used as indicators of the ecosystem they inhabit. Because ecosystems are spatially heterogeneous, and spatial patterns and processes are important to ecosystem structure and function (Babcock *et al.*, 2005), indicators on top predators should be spatially explicit for accounting for the spatial variations in the ecosystem. Here we have used spatially explicit descriptors on fishermen behavior. In the bottom-up dynamics we described, the first Fishermen component (i.e. activity budget) was significantly associated with the first components of Anchovy and Environment, and the ecological implications of these associations in several ecosystem scenarios were described previously. Therefore, fishermen PCA scores could be considered for use as ecosystem indicators of ecosystem scenarios. Interestingly, two specific fishermen movement characteristic features, namely Max.DC and k, might provide complementary characterization of the main variations on the other ecosystem compartments. However, to test for the robustness of such indicators it is necessary to rely on larger time series. Besides, strong El Niño events should be encompassed to cope with scales of variability in the NHCS that have not been included in the studied period. Larger time series would also allow detecting reference points for the statistical discrimination between ecosystem scenarios.

The pertinence of ecosystem indicators have been commonly examined through multivariate methods (e.g. Link *et al.*, 2002 and 2010) or through the discussion on their pertinence for effective management (Jennings, 2005). The use of a model – for instance, simplified food-web models (Plitzko *et al.*, 2012) could be a complementary approach to check the sensibility of data-constructed indicators. Those models would require several assumptions on relationships between the considered ecosystem compartments and other predator-prey relationships that have not been accounted for in this study. The interactions between fishermen; other top-predators competing for the same prey (e.g. seabirds and mammals; Bertrand *et al.*, 2012) and ecosystem scenarios (Pikitch *et al.*, 2004; Hooker *et al.*, 2011) should also be understood for implementing conservation plans and EAF management. For that reason, spatio-temporal data on top predators, including fishermen, are key for fisheries ecology and sustainable management of the fisheries (Hinz *et al.*, 2013).

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Appendices

Appendix A. Supplementary figures and tables for the analyses.

Figure captions.

Figure 1. Synoptic sketch of the statistical analyses.

Figure 2. Univariate series of Environment and Anchovy variables: sea surface temperature or SST (a), chlorophyll-a or CHL (b), oxycline depth or OXY (c), global biomass or s_A (d), local biomass or s_A^+ (e), index of spatial occupation or ISO (f), center of gravity of distance from the coast or DC (g), inertia of DC or I (h). Blue points correspond to winter/spring time-periods, and red points correspond to summer periods. Blue dashed lines indicate the significant winter/spring trends. Here, the time-periods at the x axes are plotted at regular steps, but the trends were actually fitted considering the real intervals between time-periods. Standard deviations of Environment variables are shown in Appendix A, Table A.1.

Figure 3. Marginal distributions and median by time-period for each Fishermen variable: fishing trip duration (a), distance traveled (b), maximum distance from the coast (c), absolute time from the beginning of the trip until the first fishing set (d), proportion of trip duration spent searching (e), proportion of trip duration spent fishing (f), proportion of trip duration spent cruising (g), shape parameter from random walk modeling (h), scale parameter from random walk modeling (i). In each subplot, the colors relate to the marginal distribution of the corresponding variable at each time-period (i.e. column). Therefore, colors represent values between 0 and 1. Each colorbar is bounded by the minimum and the maximum value of the marginal distributions comprised in the subplot. Blue solid lines indicate significant trends ($p<0.01$) over the whole studied period. Here, the time-periods at the x axes are plotted at regular steps, but the trends were actually fitted considering the real intervals between time-periods. Complete ranges of values are shown in Appendix A; here, the values associated with the highest marginal distributions are shown.

Figure 4. Time series of PCA scores for each ecosystem compartment. Percentage of explained variance are in parentheses at the top of each subplot. Red points correspond to summer time-periods and blue points to winter and spring periods. At the right side of each subplot, a label is given to each principal component. (+) and (-) symbols indicate favorable and unfavorable conditions for Fishermen, respectively. *Oxycline depth follows the seasonal cycling. But some specific events such as downwelling Kelvin wave could deepen the oxycline. **This component is only useful when comparing similar scenarios in terms of s_A, s_A^+ and DC.

Figure 5. Multiple coinertia analysis between Environment, Anchovy and Fishermen compartments. Left panel: projection of variables in the coinertia space. The definition of each variable is given in Table 2. Fishermen variables are in black, Anchovy in blue and Environment in red. Right panel: projection of time-periods in the coinertia space. Each period has three associated points, corresponding to the position of the period described by each compartment. The position of the label of each period corresponds to its location according to the synthetic table. Roman numerals and colors indicate the different clusters of time-periods.

Figure 6. Idealized 3D representation of the ecological conditions in scenarios I (2002/02-03), II (2008/02-04), III (2003/10-12) and IV (2001/10-11).
The sun or clouds and their size represent the amount of SST which for this study. Tones of blue-green color represent the amount of chlorophyll-a. Spots in dark yellow and red represent anchovy aggregations; the level of local aggregation is proportional to the darkness of the red color. Local aggregation is also represented by the amount of fish in the school. Arrows represent fishermen movements; each color is associated to a fishing trip. At the right, a table indicates the level of each variable for the given scenario. Levels can take values of: --, -, + and ++ and are associated to the values taken by each variable in Figures 2 and 3.

Tables

Table 1: Number of fishing trips corresponding to each time-period.

Time-period	Fishing trips
$2000/06-07$	5839
$2000/10-11$	5750
$2001/03-04$	7012
$2001/07-08$	865
$2001/10-11$	1612
$2002/02-03$	1368
$2002/10-11$	6409
$2003/10-12$	6262
$2004/11-12$	8983
$2005/11-12$	15252
$2006/02-04$	2990
$2006/11-12$	8593
$2007/02-04$	2395
$2008/02-04$	4611
$2008/11-12$	8604
$2009/02-04$	3151

Table 2: Description of Environment, Anchovy and Fishermen variables.

Ecosystem compartment	Variable acronym	Description	Data type	Scale of data
Environment	SST	Averaged sea surface temperature from 3°S to 16°S and from the shore up to the 2500 m isobath (in °C)	AHVRR	Monthly data
	CHL	Averaged Chlorophyll-a from 3°S to 16°S and up to the 2500 m isobath (in mg.m^{-3})	SEAWIFS and MODIS	Monthly data
	OXY	Average of oxycline depth from 7°S to 16°S (in m)	CTD and NISKIN	Scientific survey
Anchovy	s_A	Index of global fish acoustic biomass equal to $\log((\sum_{i=1}^{n} \text{NASC}_i/n) + 1)$ (in m^2.nm^{-2})	Output from acoustic surveys (Bertrand et al., 2004)	Acoustic survey
	s_{A+}	Index of local fish biomass equal to $\log((\sum_{i=1}^{n} \text{NASC}_i/n) + 1)$, $\forall \text{NASC} > 0$ (in m^2.nm^{-2})	Output from acoustic surveys (Gutierrez et al., 2007)	Acoustic survey
	ISO	Index of spatial occupation. Percentage of ESDU where anchovy is present (NASC > 0)	Output from acoustic surveys (Gutierrez et al., 2007)	Acoustic survey
	DC	Center of gravity of the distance to the coast of the acoustically observed anchovy (in km) $\text{DC} = \sum_{i=1}^{n} (\text{dc}_i \log(\text{NASC}_i + 1)) / \sum_{i=1}^{n} \log(\text{NASC}_i + 1)$	Output from acoustic surveys (Gutierrez et al., 2007)	Acoustic survey
	I	Inertia of DC (in km) $\text{I} = \sum_{i=1}^{n} (\text{dc}_i - \text{DC})^2 \log(\text{NASC}_i + 1) / \sum_{i=1}^{n} \log(\text{NASC}_i + 1)$	Output from acoustic surveys	Acoustic survey
Fishermen	Dur	Fishing trip duration (in hours)	Computed from VMS data	Fishing trip
	Dist	Distance traveled during a fishing trip (in nm)	Computed from VMS data	Fishing trip
	Max.DC	Maximum distance to the coast during a fishing trip (in nm)	Computed from VMS data	Fishing trip
	Searching	Proportion of fishing trip duration spent searching	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	Fishing	Proportion of fishing trip duration spent fishing	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	Cruising	Proportion of fishing trip duration spent cruising	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	Bef.Fishing	Absolute time from the beginning of the trip until the first fishing set (in hours)	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	k	Shape parameter from random walk modeling	Model output from VMS data (Bertrand et al. in review)	Vessel moves by season
	sigma	Scale parameter from random walk modeling	Model output from VMS data (Bertrand et al. in review)	Vessel moves by season

Notes: NASC_i: nautical-area-backscattering coefficient at i^{th} georeferenced elementary distance sampling unit (ESDU). dc_i: distance to the coast at the i^{th} ESDU.

Table 3: Significant correlations between variables and their principal components ($p < 0.05$). The percentage of explained variance of each component at each compartment is showed in italic.

Ecosystem Compartment	Variables	Components 1	2
Environment	CHL	0.93	–
	SST	0.94	–
	OXY	−0.71	−0.70
	Explained variance	75%	21%
Anchovy	s_{A^+}	0.88	–
	s_A	0.84	–
	DC	−0.87	–
	I	−0.87	–
	ISO	–	0.94
	Explained variance	60%	23%
Fishermen	Fishing	0.92	–
	k	0.70	−0.69
	Searching	0.67	–
	Dur	−0.70	–
	Max.DC	−0.78	−0.59
	Bef.Fishing	−0.81	–
	Dist	−0.83	–
	sigma	−0.86	–
	Cruising	−0.93	–
	Explained variance	71%	23%

Table 4: Correlations between variables and the multiple coinertia axes.

Variables	Axis 1 (73%)	Axis 2 (17%)
SST	0.89	0.03
CHL	0.84	0.01
OXY	−0.55	−0.64
s_A^+	0.86	0.02
s_A	0.80	0.37
ISO	−0.13	0.74
DC	−0.81	0.15
I	−0.81	0.12
Fishing	0.88	0.10
k	0.64	−0.62
Max.DC	−0.77	−0.35
sigma	−0.82	0.49
Cruising	−0.86	−0.05

Figure1

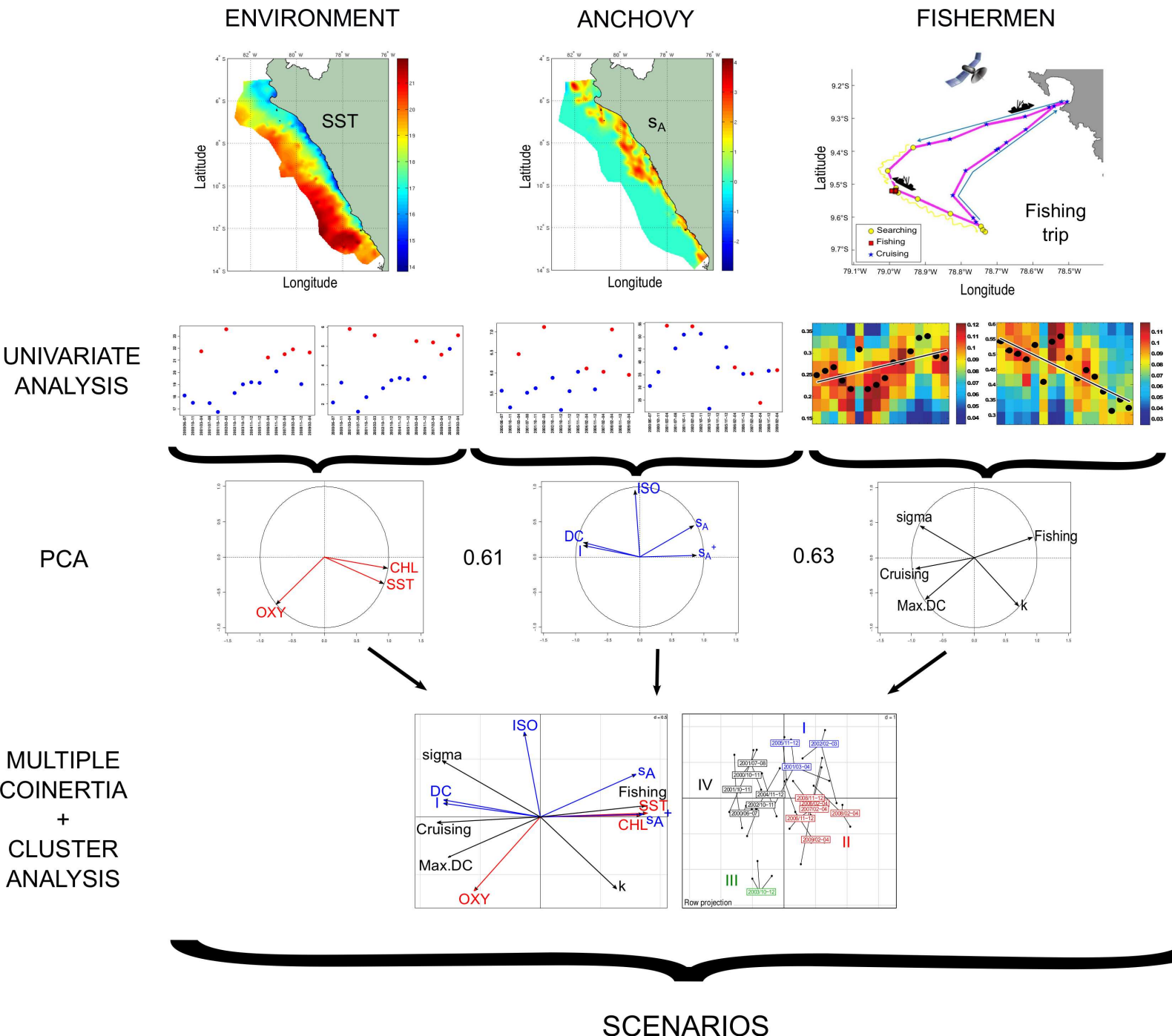

ENVIRONMENT
ANCHOVY
FISHERMEN
SST
s_A
Latitude
Longitude
Searching
Fishing
Cruising
Fishing trip
UNIVARIATE ANALYSIS
PCA
0.61
0.63
CHL
SST
OXY
ISO
DC
I
s_A
s_A^+
sigma
Fishing
Cruising
Max.DC
k
MULTIPLE COINERTIA + CLUSTER ANALYSIS
Row projection
SCENARIOS

Figure2

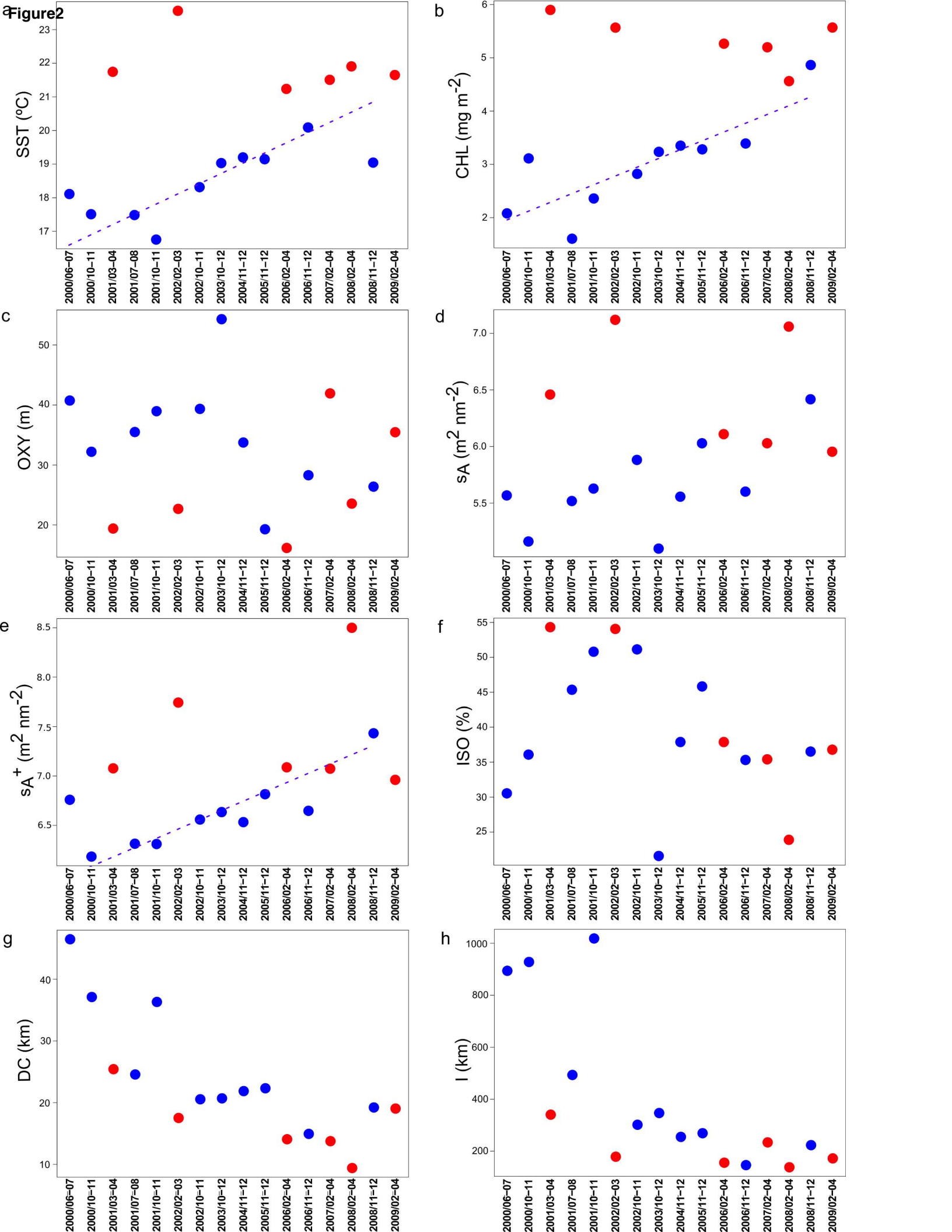

a
SST (°C)
b
CHL (mg m-2)
c
OXY (m)
d
sA (m2 nm-2)
e
sA+ (m2 nm-2)
f
ISO (%)
g
DC (km)
h
I (km)
2000/06–07
2000/10–11
2001/03–04
2001/07–08
2001/10–11
2002/02–03
2002/10–11
2003/10–12
2004/11–12
2005/11–12
2006/02–04
2006/11–12
2007/02–04
2008/02–04
2008/11–12
2009/02–04

Figure3

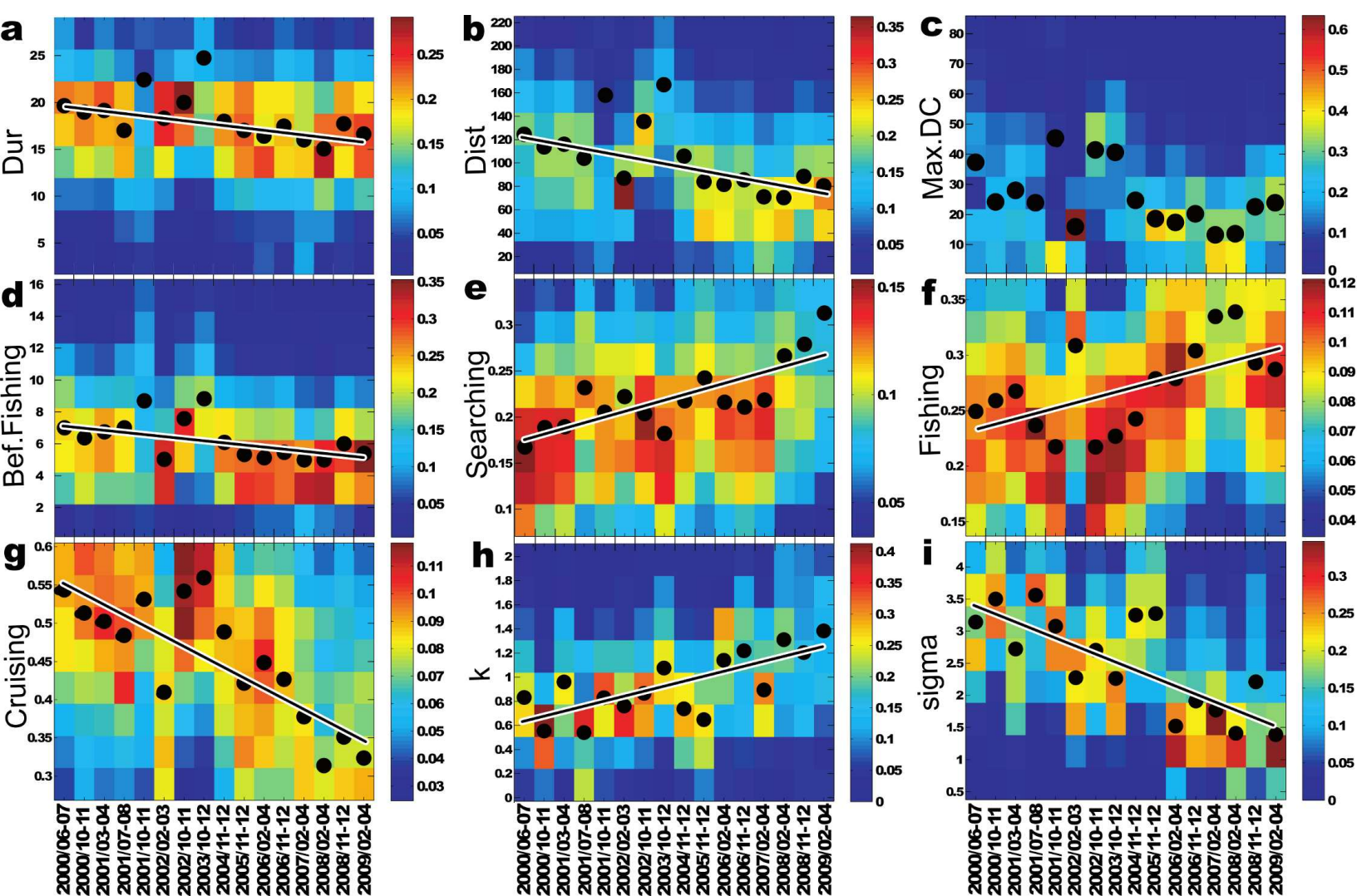
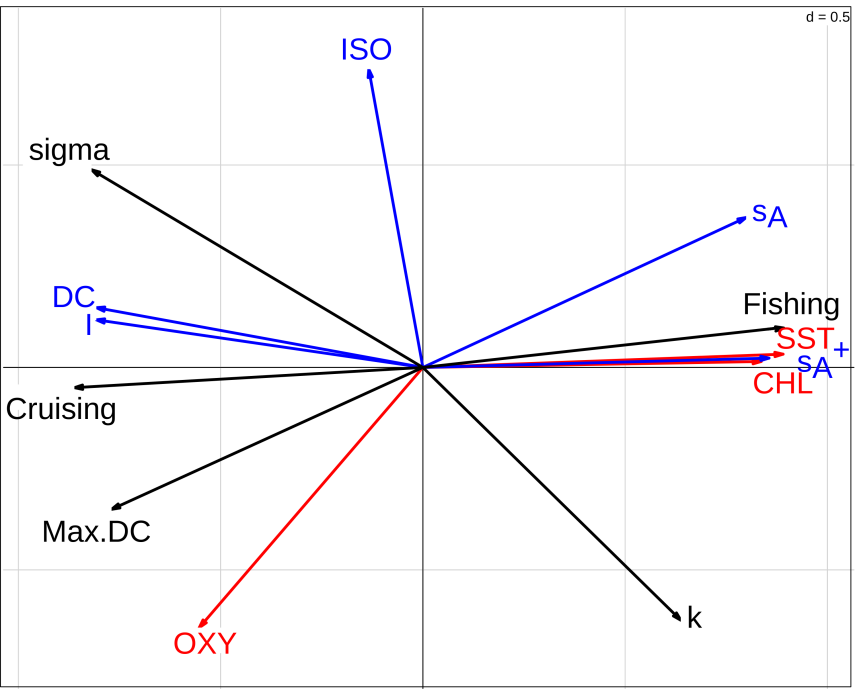

a
Dur
b
Dist
c
Max.DC
d
Bef.Fishing
e
Searching
f
Fishing
g
Cruising
h
k
i
sigma
2000/06-07
2000/10-11
2001/03-04
2001/07-08
2001/10-11
2002/02-03
2002/10-11
2003/10-12
2004/11-12
2005/11-12
2006/02-04
2006/11-12
2007/02-04
2008/02-04
2008/11-12
2009/02-04

Figure4


d = 0.5
ISO
sigma
SA
DC
I
Fishing
SST+
SA
CHL
Cruising
Max.DC
k
OXY

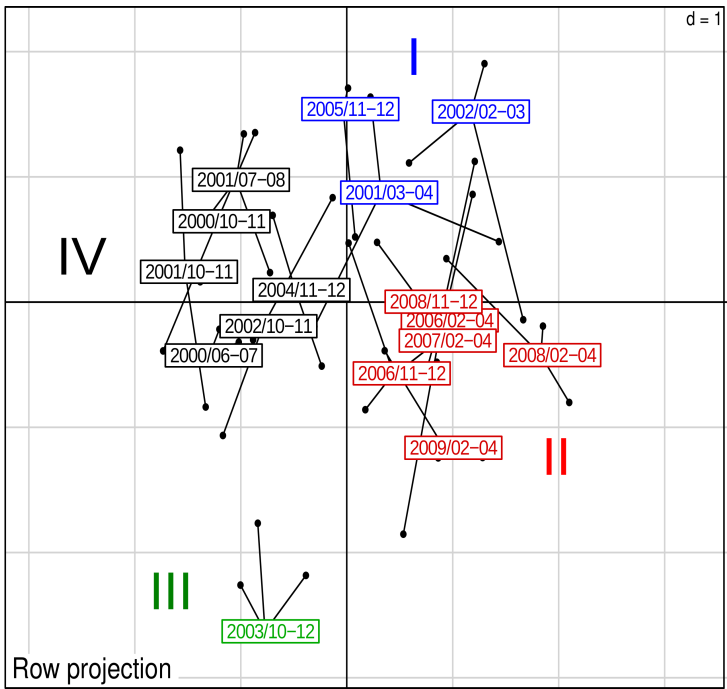
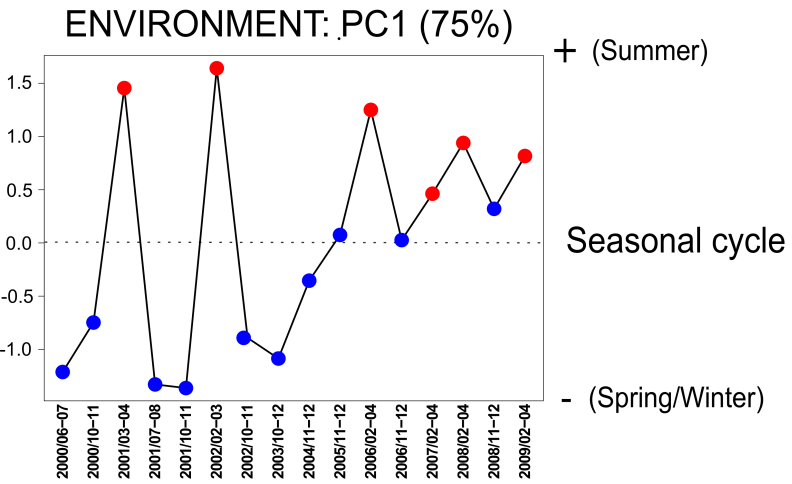
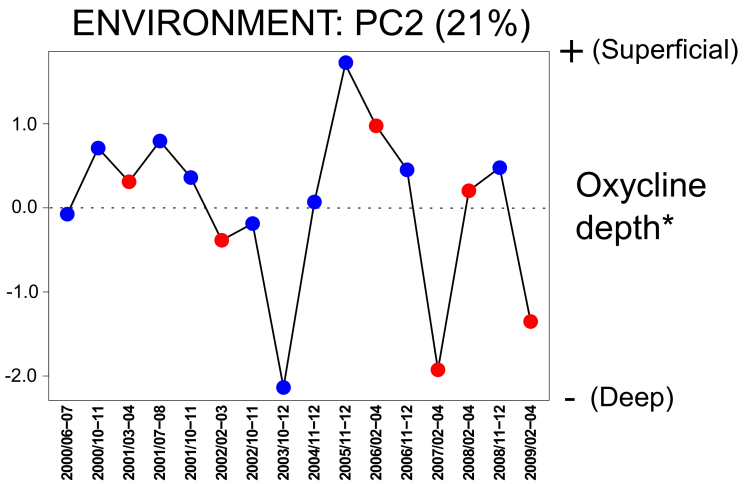
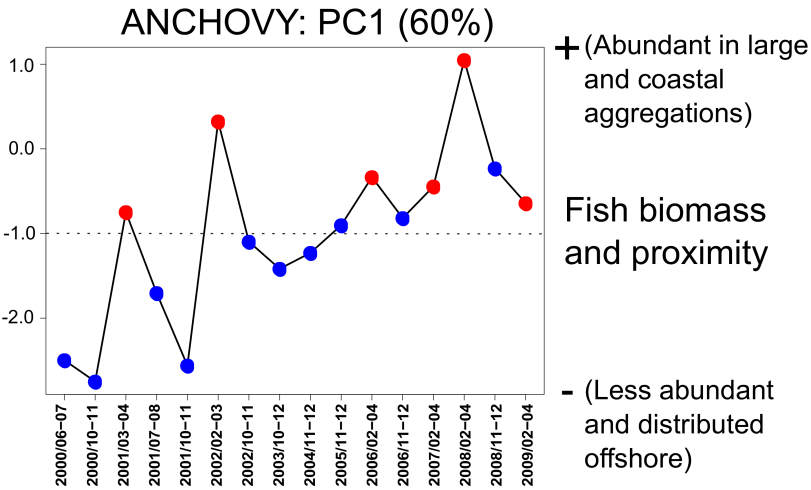
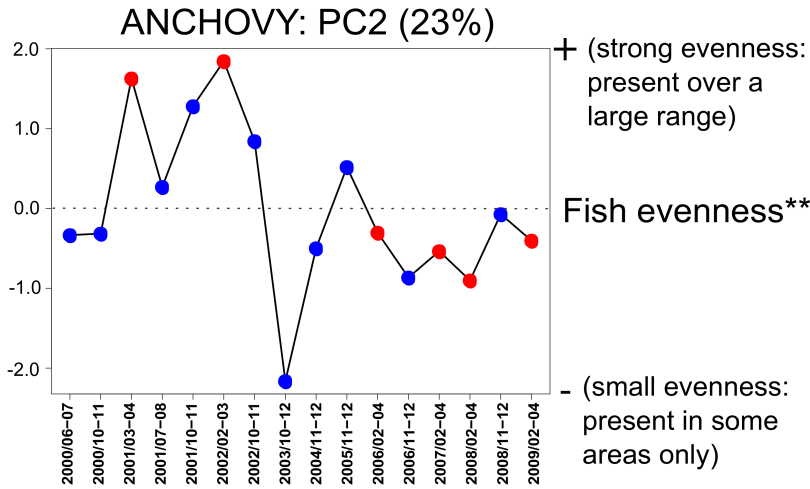

d = 1
I
2005/11−12
2002/02−03
2001/07−08
2001/03−04
2000/10−11
IV
2001/10−11
2004/11−12
2008/11−12
2006/02−04
2002/10−11
2007/02−04
2000/06−07
2008/02−04
2006/11−12
2009/02−04
II
III
2003/10−12
Row projection

Figure5


ENVIRONMENT: PC1 (75%)
+ (Summer)
Seasonal cycle
- (Spring/Winter)
1.5
1.0
0.5
0.0
-0.5
-1.0
2000/06–07
2000/10–11
2001/03–04
2001/07–08
2001/10–11
2002/02–03
2002/10–11
2003/10–12
2004/11–12
2005/11–12
2006/02–04
2006/11–12
2007/02–04
2008/02–04
2008/11–12
2009/02–04


ENVIRONMENT: PC2 (21%)
+ (Superficial)
Oxycline depth*
- (Deep)
1.0
0.0
-1.0
-2.0
2000/06–07
2000/10–11
2001/03–04
2001/07–08
2001/10–11
2002/02–03
2002/10–11
2003/10–12
2004/11–12
2005/11–12
2006/02–04
2006/11–12
2007/02–04
2008/02–04
2008/11–12
2009/02–04


ANCHOVY: PC1 (60%)
+ (Abundant in large and coastal aggregations)
Fish biomass and proximity
- (Less abundant and distributed offshore)
1.0
0.0
-1.0
-2.0
2000/06–07
2000/10–11
2001/03–04
2001/07–08
2001/10–11
2002/02–03
2002/10–11
2003/10–12
2004/11–12
2005/11–12
2006/02–04
2006/11–12
2007/02–04
2008/02–04
2008/11–12
2009/02–04


ANCHOVY: PC2 (23%)
+ (strong evenness: present over a large range)
Fish evenness**
- (small evenness: present in some areas only)
2.0
1.0
0.0
-1.0
-2.0
2000/06–07
2000/10–11
2001/03–04
2001/07–08
2001/10–11
2002/02–03
2002/10–11
2003/10–12
2004/11–12
2005/11–12
2006/02–04
2006/11–12
2007/02–04
2008/02–04
2008/11–12
2009/02–04

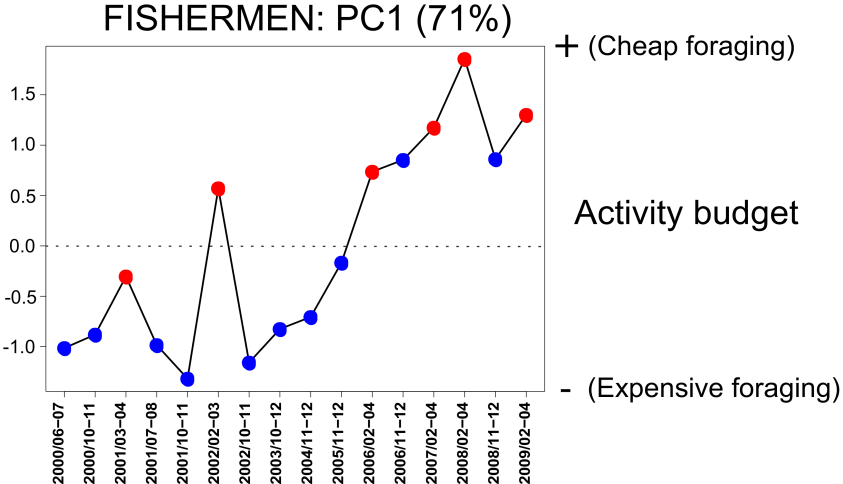

FISHERMEN: PC1 (71%)
+ (Cheap foraging)
Activity budget
- (Expensive foraging)
1.5
1.0
0.5
0.0
-0.5
-1.0
2000/06–07
2000/10–11
2001/03–04
2001/07–08
2001/10–11
2002/02–03
2002/10–11
2003/10–12
2004/11–12
2005/11–12
2006/02–04
2006/11–12
2007/02–04
2008/02–04
2008/11–12
2009/02–04

Figure6

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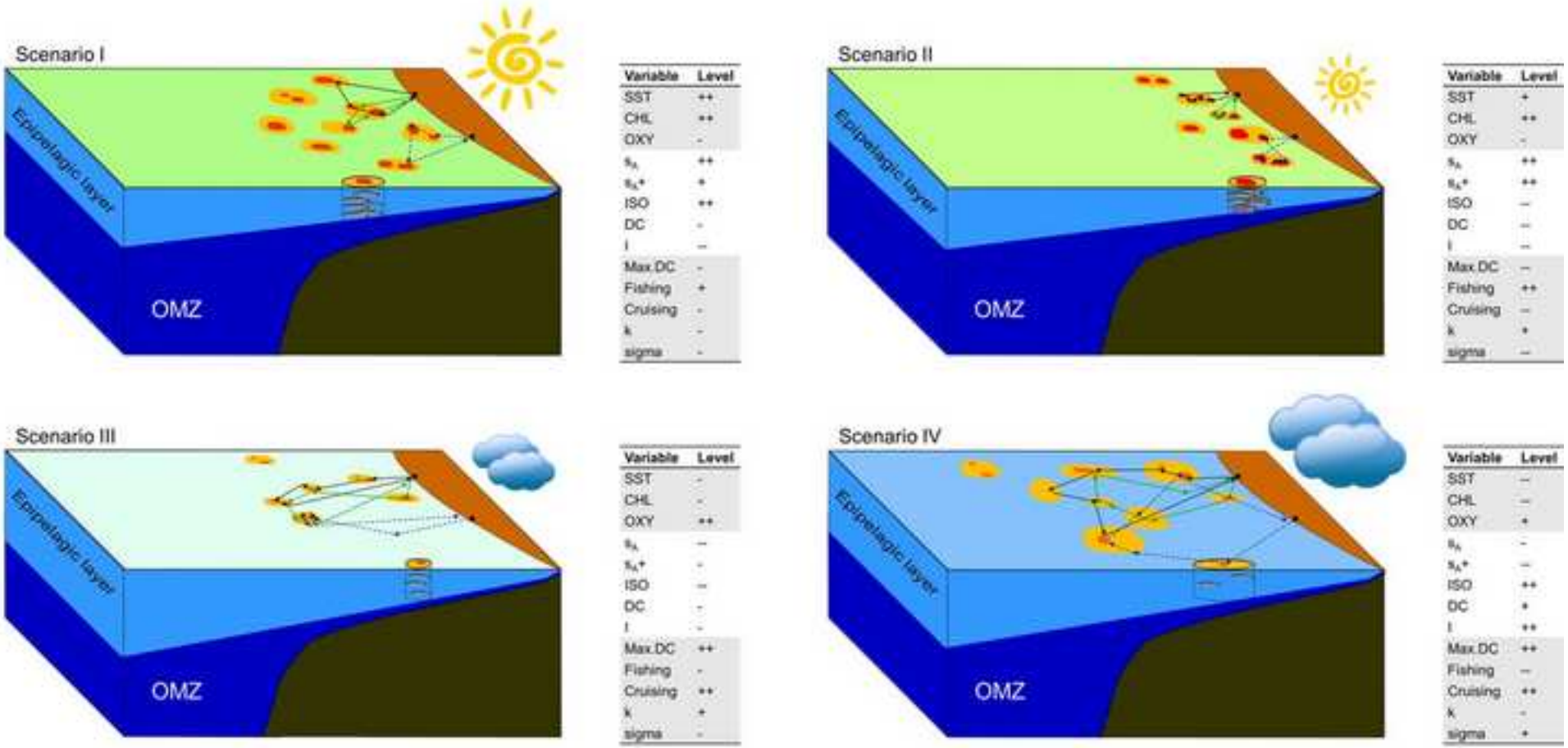

Supplementary Material

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